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13. ABSTRACT (Maximum 200 words) We have pioneered methods for using modern, high-resolution sampling technology (the Optical Plankton Counter, or OPC) to:  (1) Demonstrate the strong relationship between physical forcing and zooplankton distributions at the mesoscale. Our studies in the California Current show that zooplankton distributions and dynamics are strongly forced by mesoscale features such as eddies and jets. This scale of interaction has gone entirely unobserved by the 50-year long CalCOFI program due to sampling bias.  (2) Develop a new method, based on biomass spectral theory, for estimating the productivity of zooplankton at high spatial and temporal resolution. This method utilizes data gathered from OPC, and can be applied easily and rapidly. Our example of application in the California Current demonstrated low productivity in the central jet, and higher productivity in the eddy region immediately adjacent to the jet.  (3) Elucidate the mechanism of "biological attraction," a biological force that acts to counter dispersive physical forces, and thus to maintain aggregations of single species on fine scale (100s of meters). We developed the theory and demonstrated its application, again with modern sampling technology (ADCP).  The successful completion of this project has clearly demonstrated the application of several modern biological measuring devices that can be effectively deployed at the same temporal and spatial scales as might be common in physical oceanography. The conjunction of these methods with concurrent physical measurements is an extremely powerful tool for understanding marine ecosystems.				
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**Final Technical Report**  
**Physical Forcing of Zooplankton Dynamics**  
**(Agreement No: N001-92-J-1618)**

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## **LONG TERM GOALS**

The long-term goals of our laboratory were to develop and apply new methods for sampling and assessing the bioenergetics of zooplankton. We want to be able predict the distribution of zooplankton, particularly in relation to physical fluid dynamics at the mesoscale and below.

## **SCIENTIFIC OBJECTIVES OF THIS EFFORT**

Our research project is aimed at understanding how the non-linear dynamics of mesoscale eddies and jets force the abundance, distribution and turnover rates of zooplankton populations in the sea. We have specifically focused on the California Current.

## **APPROACH**

We participated in two interdisciplinary cruises off northern California in the spring and summer of 1993, in which a variety of new instruments were deployed on an undulating, towed body (the SeaSoar) to sample the upper ocean (0-300 m) at high resolution to survey a 100,000 km<sup>2</sup> region. Our approach was to employ a new instrument, the Optical Plankton Counter, to measure the size-frequency distributions of zooplankton in time and space. This approach was supplemented by net catches of zooplankton for calibration purposes.

## **TASKS ACCOMPLISHED**

### **1. Data analysis**

After completion of the survey cruises, we spent approximately two years analyzing data from the two cruises, focusing on results of the large-scale survey (a small-scale survey was also carried out on both cruises). Several gigabytes of data were collected. These were processed to produce a standardized data set, which included data on physics and optics in addition to our own zooplankton data. The standardized OPC data set has the following resolution on the following

scales: 5 km in the horizontal, 10 m in the vertical, and 60 size categories of zooplankton in the size range from 3-3,000  $\mu\text{g}$  carbon body weight.

## 2. Publication

Three significant publications emerged from this study. Each publication represents, we believe, a fundamental advance in the theory and understanding of zooplankton and their interaction with their physical fluid environment. The substance of these publications are described in the following section, below.

## RESULTS

### (a) Physical forcing of zooplankton distributions

In this paper (*Journal of Marine Research*, **53**: 647-674) we showed that mesoscale zooplankton aggregations are strongly linked to dynamic physical features. In the California Current, these features are principally eddies and jets. Highs and lows in zooplankton abundance occur on precisely the same scales as eddies and jets, and are persistent for time scales of a few months.

In a historical vein, it is interesting to note that the dominant scale of distribution we observed has been totally unobservable by the 50-year CalCOFI time-series. A forthcoming paper (submitted) will address the aliasing of purportedly "mesoscale" surveys (such as the large scale EBC surveys) by inadequate consideration for the time-scales of circulation. We use an EOF method to show how this aliasing occurs, and to quantify its magnitude.

### (b) Biological attraction – an explanation for zooplankton small-scale patchiness

In this paper (*Journal of Marine Research*, **54**: 1017-1037), we use measurements of zooplankton aggregations made with ADCP to demonstrate the application of the theory of "biological attraction," a measurable force that acts to counter diffusive and advective dispersion of zooplankton species and thus serves as a positive force that maintains zooplankton patches on scales of hundreds of meters. The force of biological attraction was defined, and a method for measuring it (in units of Newtons) was put forward using field data.

### (c) Zooplankton productivity on the mesoscale, estimated using Optical Plankton Counter

In this paper (*Marine Ecology Progress Series*, **159**: 61-73) we developed a new method to estimate the production rate of zooplankton, based on field measurements obtained with the Optical Plankton Counter. The method is based on biomass spectral theory, similar to that developed by Trevor Platt and Ken Denman in the late 1970s. In our opinion, fortified by critical examination by scholars in the area of zooplankton productivity, the Platt-Denman theory is fundamentally flawed

by a critical assumption that the turnover rate of individuals can be considered equal to the turnover rate of biomass (the "turnover rate assumption"). The two parameters have identical dimensions, but this assumption is a common error in a number of publications in the field. It has been shown conclusively that the turnover rate assumption is wrong, and leads to the propagation of significant errors. We corrected this assumption and derived a new set of equations that allow the estimation of zooplankton productivity from raw data gathered on the biomass spectrum.

One very important result of our analysis is that the slope of the biomass spectrum is defined as the ratio of mortality to growth. The value of the biomass spectrum thus indicates whether there is net accumulation or disappearance of zooplankton at any given location or a given time. The instantaneous value is compared to either a global spatial average or a global temporal average, depending upon the investigator's interest (i.e. spatial or temporal variability).

We applied the method to the data set gathered in this ONR project in the California Current. One most interesting finding was that, in summer, the central jet of the northern California Current is a zone of net mortality, surrounded on either side by zones of net increase. At a scale of 1-2 Rossby radius' distance from the central jet, productivity again becomes negative. This result, while entirely unanticipated, is understandable in the light of what we know about the physical dynamics of the region and how the known zooplankton species might respond to strong transport (jet) or maintenance in a zone of high primary productivity (eddies adjacent to the central jet).

## IMPACT FOR SCIENCE OR SYSTEMS APPLICATIONS

### 1. Impact on systems applications

Zooplankton are significant acoustic targets at certain frequencies, especially in the range from ca. 100 kHz to 2MHz. If our observations are generally true, then one would expect the variability in acoustic backscatter at these frequencies to be strongly correlated with the distribution of mesoscale eddies.

### 2. Impact on understanding zooplankton dynamics of the California Current

Zooplankton studies were originally incorporated into the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program on the supposition that their distribution might provide a key to understanding the distribution of target fishes (sardines and anchovies). The typical station spacing in offshore waters of the CalCOFI program is 45 nautical miles. It is clear from our results that the CalCOFI level of resolution is inadequate to characterize the distribution of zooplankton in the California Current.

### 3. Impact on estimation of zooplankton production

We developed a remarkably rapid, easy, and highly resolving method to estimate zooplankton production using modern instrumentation (the OPC, or Optical Plankton Counter). This method is theoretically sound, easy to apply, and more highly resolving in space and time than any method of which we are aware. Resolving spatial and temporal variability has been the central problem in estimates of zooplankton production. This ONR-funded program made it possible to make such a breakthrough, that has been waiting for more than 50 years to be solved. We believe the method we have developed is robust and will prove to be a foundation from which others can work for some time into the future.

## RELATIONSHIP TO OTHER PROJECTS

### ADCP estimates of zooplankton metabolism

Under another ONR award we investigated the potential of the ADCP to provide a proxy of zooplankton metabolism. This was approached from the knowledge that the second moment of Doppler shift provides a measurement of swimming speed of the acoustic target. Because swimming speed is proportional to animal active metabolism, we are analyzing the relationship between ADCP data products and direct measurements of zooplankton metabolism. If this approach works well, then we will have developed a non-invasive, synoptic method for evaluating the community metabolism of marine zooplankton. This project is related through the common interest in assessing zooplankton biomass via ADCP backscatter.

## LIST OF PUBLICATIONS

### Published

- 1994 *Calanoides acutus* (Giesbrecht) in Gerlache Strait, Antarctica II. Solving an inverse problem in population dynamics. *Deep-Sea Research II*, **41**:209-227. [M.E. Huntley, M. Zhou and M.D.G. Lopez]

Elemental composition, metabolic activity and growth of Antarctic krill, *Euphausia superba* Dana, during winter. *Marine Ecology Progress Series*, **107**:23-40. [M.E. Huntley, W. Nordhausen and M.D.G. Lopez]

ADCP measurements of the distribution and abundance of euphausiids near the Antarctic Peninsula in winter. *Deep-Sea Research I*, **41**:1425-1445. [M. Zhou, W. Nordhausen and M. E. Huntley]

- 1995 Mesoscale distribution of zooplankton in the California Current in late spring, observed by Optical Plankton Counter. *Journal of Marine Research*, **53**: 647-674 [M. E. Huntley, M. Zhou and W. Nordhausen]

Physical control of population dynamics in the Southern Ocean. *ICES Journal of Marine Science*, **52**: 457-468. [M. E. Huntley and P. P. Niiler]

- 1996 Temperature and copepod production in the sea: a reply. *American Naturalist*, **148**: 407-420. [M.E. Huntley]

The principle of biological attraction, demonstrated by the bio-continuum theory of zooplankton patch dynamics. *Journal of Marine Research*, **54**: 1017-1037. [M. Zhou and M.E. Huntley]

- 1997** Population dynamics theory of plankton based on biomass spectra. *Marine Ecology Progress Series*, **159**: 61-73. [M. Zhou and M.E. Huntley]

## **COLLABORATORS:**

Dr. Meng Zhou, Scripps Institution of Oceanography

Dr. Walter Nordhausen, Scripps Institution of Oceanography

Dr. Mai Lopez, University of Hawaii

Dr. Francois Carlotti, Station Zoologique, Villefranche-sur-Mer, France

Dr. Silvia Pinca, University of Genoa, Italy

## **GRADUATE STUDENTS: 0**

## **PATENTS: 0**

## **PRESENTATIONS**

### **1993**

"Biological and physical dynamics in an eastern boundary current," Departmental Seminar, School of Ocean & Earth Science and Technology, University of Hawaii, Honolulu (November)

### **1994**

"Mesoscale and small-scale distributions of zooplankton using the Optical Plankton Counter," 1994 AGU Ocean Sciences Meeting, San Diego (Feb)

"Elemental composition, metabolic activity and growth of Antarctic krill during winter," [co-authors: W. Nordhausen & M. Lopez] 1994 AGU Ocean Sciences Meeting, San Diego (Feb)

- "Diel vertical migration and feeding of *Metridia gerlachei* during spring," [co-authors: W. Nordhausen & M. Lopez] 1994 AGU Ocean Sciences Meeting, San Diego (Feb)
- "Statistical mechanics of animal patches: Theories and observations," [co-author M. Zhou] 1994 AGU Ocean Sciences Meeting, San Diego (Feb)
- "*Calanoides acutus* in Gerlache Strait, Antarctica: solving an inverse problem in population dynamics," [co-author M. Zhou] 1994 AGU Ocean Sciences Meeting, San Diego (Feb)
- "Physical control of population dynamics in the Southern Ocean," Invited Speaker, ICES Symposium on Zooplankton Production, Plymouth, UK (Aug)

## 1995

- "Mesoscale dynamics of zooplankton in the Pacific Ocean," Marine Biology Seminar Series, Scripps Institution of Oceanography (Jun)

## 1996

- "Zooplankton dynamics in a mesoscale eddy-jet system off California," [co-authors M. Zhou, Y. Zhu and A. Gonzalez] 1996 AGU Ocean Sciences Meeting, San Diego (Feb)
- "The influence of animals on turbulence in the sea," [co-authors M. Zhou, X. Zhong] 1996 AGU Ocean Sciences Meeting, San Diego (Feb)
- "Space-time variability of zooplankton-sized particle concentrations at the Hawaii Ocean Time-series station (Station ALOHA)," [co-authors M. Lopez, Y. Zhu] 1996 AGU Ocean Sciences Meeting, San Diego (Feb)
- "A new model of zooplankton population dynamics using the biomass spectrum," [co-author M. Zhou] 1996 AGU Ocean Sciences Meeting, San Diego (Feb)
- "Calibrated bioacoustic measurements of zooplankton using ADCP," [co-authors W. Nordhausen, M. Zhou] 1996 AGU Ocean Sciences Meeting, San Diego (Feb)
- "Mesoscale dynamics of zooplankton in the California Current in summer, in relation to physical circulation," [co-authors S. Pinca, Y. Zhu, M. Zhou] 1996 AGU Ocean Sciences Meeting, San Diego (Feb)

## SERVICE ON COMMITTEES/PANELS

- Convener, Special Session on Eastern Boundary Current Dynamics, AGU/ASLO Ocean Sciences Meeting, San Diego, CA Feb 21-25, 1994.
- Member, Planning Group for Biogeochemical Cycles, SCAR Group of Specialists on Global Change and the Antarctic, 1994
- Invited Keynote Speaker, Symposium on Zooplankton Production, Plymouth, UK, Aug 1994
- Member, (elected) Steering Committee, GLOBEC, January, 1989 - present
- Member, GLOBEC Working Group on Technology, May, 1989 - present

Member, GLOBEC Executive Committee, Sep 1990 - present  
Chairman, GLOBEC Outreach Committee, 1993-1996  
Member, Executive Committee, ONR Eastern Boundary Current initiative, Oct 1992-1997  
International Liaison between US GLOBEC and GLOBEC International Scientific Steering  
Committees, Mar 1993 - 1996  
Co-editor, Zooplankton Methodology Manual (with H.-R. Skjoldal and J. Lenz), under the  
auspices of ICES (International Council for the Exploration of the Sea), Mar 1994-  
present  
Member, Planning Group for Biogeochemical Cycles, SCAR Group of Specialists on Global  
Change and the Antarctic, 1994-1995  
Member, Scientific Committee, International JGOFS Symposium on Carbon Fluxes, Brest,  
France, 1994-1995  
Member, Organizing Committee, Ocean Optics XIV Conference (Kona, Hawaii; Nov 1998),  
Nov 1997-present.